Pedobiologia, Bd. 6, S. 238—243 (1966)

Rothamsted Experimental Station, Harpenden, Herts

Studies in leaf-litter breakdown II Breakdown rate of "sun" and "shade" leaves

By G. W. Heath and Margaret K. Arnold

With 4 figures in the text

(Received February 16th, 1966)

Synopsis

Original scientific paper · Wissenschaftliche Originalmitteilung

Oak leaves (*Quercus robur*) and beech leaves (*Fagus sylvaticus*) collected at leaf-fall were arbitrarily divided into hard and soft categories. These categories are thought to be synonymous with "sun" and "shade". Disks of the selected leaves were laid on the soil surface of treated plots in oak and beech woodland. One treatment excluded earthworms, the other did not. Samples of leaf disks were collected regularly and the area of leaf lamina that had disappeared estimated. Soft leaf disks disappeared faster than hard ones. The disks go faster when exposed to earthworms' feeding, and oak goes faster than beech. From January to June worms seem to remove more leaf material from the surface by burying it than by eating it. They bury soft leaves in preference to hard ones.

Nach dem Blattfall gesammelte Eichenblätter (*Quercus robur*) und Buchenblätter (*Fagus sylvaticus*) wurden willkürlich in zwei Gruppen geschieden, in „harte" (dicke) und „weiche" (dünne) Blätter. Es wurde angenommen, daß diese Gruppen den „Sonnen-" und „Schattenblättern" entsprachen. Kreisrunde Scheiben dieser ausgesuchten Blätter wurden auf der Bodenoberfläche von präparierten Versuchsflächen in einem Eichen- und einem Buchenwald ausgelegt. Auf den einen Versuchsflächen waren die Regenwürmer ausgeschlossen, auf den anderen nicht. Von den ausgelegten Blattscheiben wurden regelmäßig Proben eingesammelt, um den Rotteschwund planimetrisch zu bestimmen. Weiche Blätter schwinden schneller als harte. Die Blattscheiben schwinden schneller, wenn Regenwürmer Zugang zu ihnen haben und Eichenblätter schwinden rascher als Buchenblätter. Von Januar bis Juni scheinen die Regenwürmer mehr Blattmaterial durch Vergraben von der Bodenoberfläche fortzuschaffen als durch Fraß. Die Regenwürmer graben weiche Blätter im Vergleich zu harten bevorzugt ein.

Contents

1. Introduction

During our work on leaf breakdown we noticed that the condition of the leaf, when exposed to attack by soil organisms, greatly influenced rate of breakdown (Edwards and Heath, 1963). Leaf-disks collected and buried in the soil during July all gradually and uniformly changed colour from green to brown, whereas leaves collected from trees in September changed colour at differing times after burial. Some leaves picked in September stayed green and were soon attacked by soil animals; they seemed softer and thinner than others which soon turned brown and were little attacked even after nine months. All these leaves had been collected randomly and we suspected the soft leaves were "shadow" leaves and the hard ones were "sun" leaves. Van der Drift (1965) states that thin, shade

leaves are attacked earlier than thick, sun leaves, and HILLIS and SWAIN (1959) showed that leaves from the shady part of the Victoria plum (*Prunus domestica* var. *Victoria*) contain fewer phenolic substances than leaves from the sunny part.

The experiments now described were made in two types of woodland, to compare the rate of breakdown of sun and shade leaves, i. e. "hard" and "soft" leaves, (selected after leaf fall) in the presence and absence of earthworms.

2. Material and methods

Freshly fallen oak and beech leaves were collected from the ground of an oak-dominant woodland and a 20-year old beech plantation during November/December 1962. They were arbitrarily sorted into "hard" and "soft" categories, and disks of 2.5 cm diameter were cut from them. Leaves which fitted neither category were discarded. Experimental sites were then prepared in each woodland.

Plots of 60 cm square were marked out and the surface litter removed. For one treatment ("A") the top 7.5 cm of soil was removed and hand-sorted to eliminate earthworms and their cocoons. Terylene net (1 mm mesh) was laid on the earth, to prevent earthworms re-entering from below, and the worm-free soil replaced. For the other treatment ("B") the soil was left undisturbed. There were 4 replicates of each treatment and therefore eight plots in each woodland. Each treatment plot was then split into two halves and 250 hard disks laid on one half of the surface and 250 soft disks on the other (Fig. 1). The disks on all plots were covered by terylene netting (0.5 cm mesh) and the litter replaced on this: the netting could be lifted to examine or collect disks during the experiment.

Oak disks were laid on the plots in late December, 1962. After this severe weather and snow cover made experimental work impossible until early March, 1963, when the beech disks were laid on the plots and observations began on the oak disks. Samples of 20 hard and 20 soft disks were then collected at monthly intervals from each plot at both sites until November, when all the disks had been taken. In the plots containing earthworms,

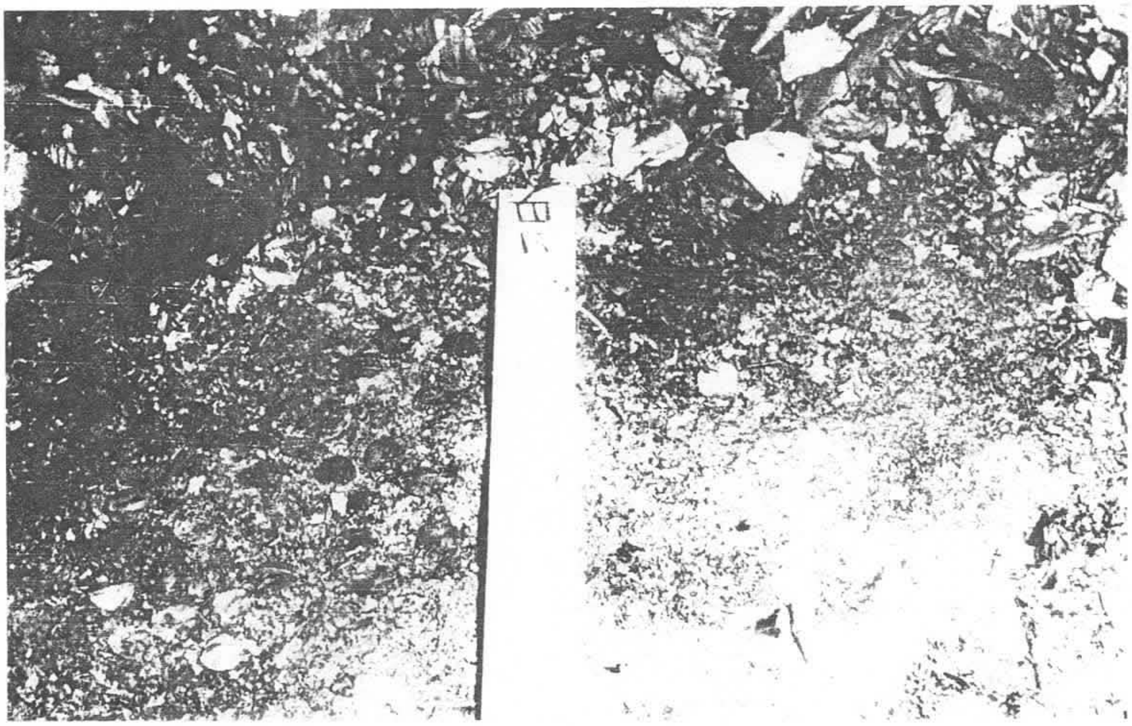

Fig. 1. Leaf disks laid on the surface "B" plots. **H** are hard disks, **S** are soft disks. Note that after 3 months practically no **S** disks are left.

earthworms not only fed on the disks but also completely removed some of them, so the disks remaining in these plots were counted at each inspection.

The samples were all stored in polythene bags at —5 °C. At the end of the experiment the area of lamina disappeared from the disks was estimated photometrically (HEATH, EDWARDS and ARNOLD, 1964). The disks were then oven dried at 90 °C, ground in an analytical ball mill and stored for chemical analysis.

3. Results and discussion

Mean figures for the percentage of leaf lamina that disappeared from the disks are in Table 1, and figures 2 and 3 were plotted from these measurements. Both graphs show that soft leaves disappeared faster than hard ones, and earthworms speed the disappearance of both types of leaf. Table 2 gives the number of disks removed by earthworms at each sampling date, expressed as a percentage of the number of disks then remaining, and these values were used to plot the graph in figure 4. As previously shown (EDWARDS and HEATH, 1963), oak leaves are removed faster than beech. Comparing figure 4 with figures

Table 1 Relative (%) disappearance of lamina from oak and beech disks.

Date 1963	Oak A soft	Oak A hard	Oak B soft	Oak B hard	Beech A soft	Beech A hard	Beech B soft	Beech B hard
Mar. 8	0.5	0.0	3.8	0.0	.	.	.	.
April 9	13.5	5.6	11.8	3.4	5.3	0.8	3.8	0.8
May 8	13.8	1.6	32.8	6.0	5.5	2.8	9.8	2.0
June 7	68.0	2.3	63.0	28.0	6.0	0.0	9.0	6.0
July 5	17.0	4.0	86.8	33.5	14.8	1.0	38.5	5.0
Aug. 2	24.5	10.8	100.0	65.6	15.0	6.0	95.0	9.8
Aug. 30	25.8	19.3	.	88.0	10.8	10.0	100.0	35.0
Sep. 27	32.3	18.3	.	—	10.8	6.5	.	48.8
Oct. 24	45.4	12.8	.	.	39.0	7.5	.	100.0
Nov. 22	91.0	39.3	.	.	68.5	8.8	.	.

A — earthworms absent B — earthworms present

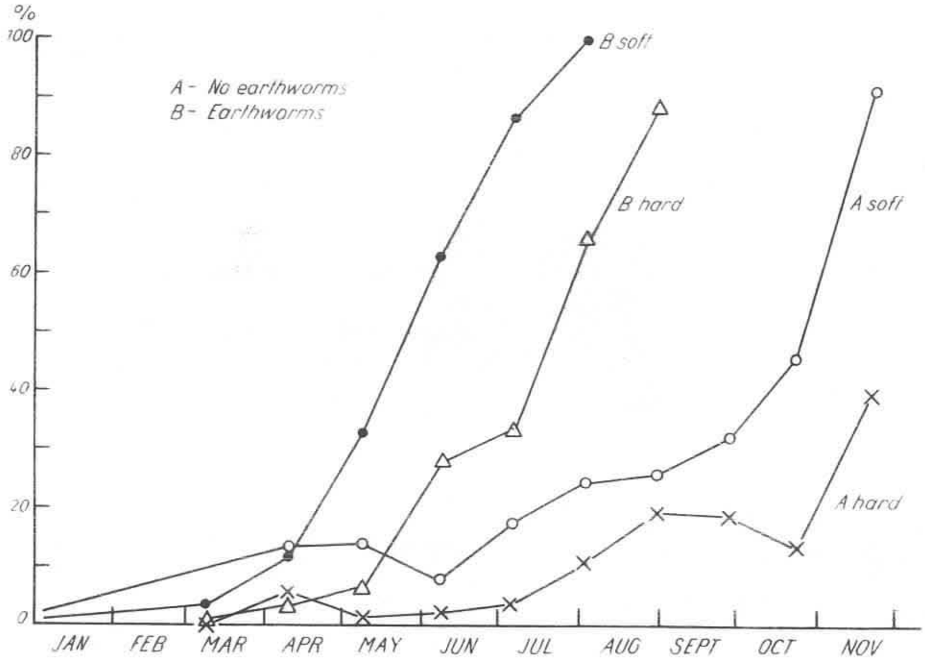

Fig. 2. Relatige % disappearance of lamina from oak discs. (Experiment started with all 4 treatments in December. First measurement in March.)

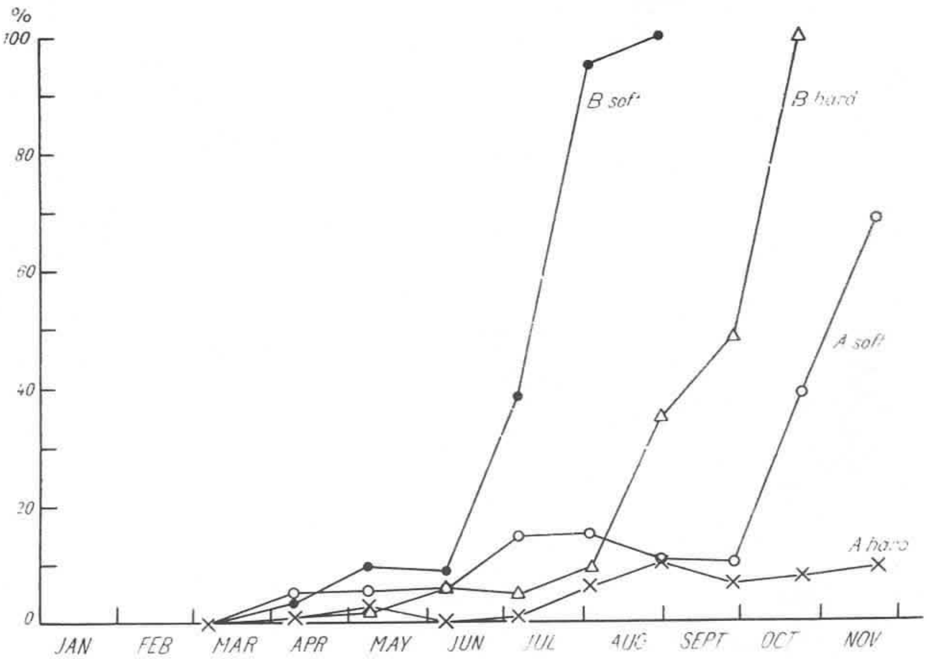

Fig. 3. % disappearance of lamina from beech discs.

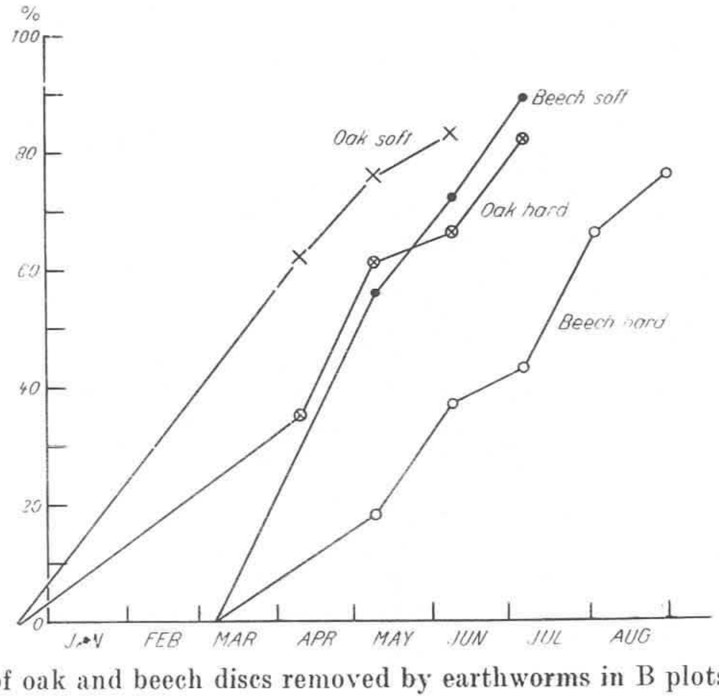

Fig. 4. % number of oak and beech discs removed by earthworms in B plots.

2 and 3 suggests that earthworms remove more leaf material from the soil surface during the first half of the year by burying it than by eating it on the soil surface; most burying is probably done by the species *Lumbricus terrestris*. Figure 3 shows that earthworms buried more soft leaves of both species than hard ones.

Lumbricus terrestris uses leaves to line its burrow, so soft leaves, which are more flexible, are probably selected for this rather than hard ones. Burial in the soil keeps the leaves moist, which encourages microbial activity and probably renders them more palatable to earthworms. Soft leaves apparently become acceptable as food for earthworms and other soil animals sooner than hard ones, because soft leaves diappear faster from the soil surface, both by being buried and by having the lamina removed. The texture of leaves

depends on their structure; the lignin content may be important, according to KING and HEATH (in prep.), who analysed samples from these experiments. Beech leaves contained more lignin than oak leaves; if this does reflect texture then it correlates with the result that oak leaves always disappear faster than beech leaves. KING and HEATH (in prep.) found only quantitative differences in composition between hard and soft leaves, with significantly more polyphenols and total nitrogen in hard than in soft leaves. The differences in nitrogen content disappear after the leaves have been in the litter layer for 8 weeks.

Palatability probably depends on polyphenol and sugar content. HEATH and KING (1964) thought that the palatability of oak leaves increased as their polyphenol content decreased. Throughout our experiments KING and HEATH (in prep.) found hard beech leaves to contain more polyphenols than soft ones. See Table 2 in part III of thresaries.

Table 2 Relative (%) number of oak and beech disks removed by earthworms in B plots.

Date 1963	Oak		Beech	
	soft	hard	soft	hard
April 9	62	35	no determination	no determination
May 8	76	61	56	18
June 7	83	66	72	37
July 6	—	82	89	43
Aug. 2	.	81	—	66
Aug. 30	.	—	.	76

HANDLEY (1961) suggested that phenolic compounds precipitate protein complexes. rendering the residual leaf proteins resistant to decomposition and forming a protective layer on the cellulose of the cell walls in tanned leaves. This has previously been considered a possible reason why such leaves might be difficult to digest and therefore are often not eaten by soil animals. However, OVERGAARD NIELSEN (1962), who studied the digestive enzymes of a wide taxonomic range of soil invertebrates, found xylanase and pectinase in only a few species of Dipterous larvae and in the Mollusca, which also possess cellulase. whereas cellulase, xylanase and ligninase are widely distributed in the soil. We therefore agree with other workers (BURGES, 1965 and VAN DER DRIFT, 1965) that primary chemical breakdown of plant structural polysaccharides in leaf litter is probably the work of the soil microflora, and that the initial role of soil animals in litter breakdown is comminution and incorporation of debris into the soil.

The food preferences of soil fauna probably depend on the palatability of leaf material rather than on its digestibility, and it is interesting to note that WILKINS et al. (1953) found tannin made the herbage of *Sericea lespedeza* less palatable to sheep. The unpalatability of leaf material rich in polyphenol may be because of its astringence. Soft leaves contain less polyphenol than hard ones and are more palatable to soil animals.

4. Literature

BURGES, N. A., 1965. Biological processes in the decomposition of organic matter. In: Experimental Pedology, ed. E. G. HALLSWORTH and D. V. CRAWFORD, Butterworth. London.

DRIFT, J. VAN DER, 1965. The effects of animal activity in the litter layer. In: Experimental Pedology, ed. E. G. HALLSWORTH and D. V. CRAWFORD. Butterworth. London.

EDWARDS, C. A., and G. W. HEATH, 1963. The role of soil animals in breakdown of leaf material. In: Soil Organisms, ed. J. DOEKSEN and J. VAN DER DRIFT. North-Holland Publishing Company. Amsterdam.

HANDLEY, W. R. C., 1961. Further evidence for the importance of residual leaf protein complexes in litter decomposition. Plant and Soil, **15**, 37—74.

HEATH, G. W., C. A. EDWARDS and M. K. ARNOLD, 1964. Some methods for assessing the activity of soil animals in the breakdown of leaves. Pedobiologia, **4**, 80—87.
— and H. G. C. KING, 1964. Litter breakdown in deciduous forest soils. VIII Int. Soil Sci. Congress. Bucharest.
HILLIS, W. E., and T. SWAIN, 1959. The phenolic constituents of *Prunus domestica* II. The analysis of tissues of the Victoria plum tree. J. Sci. Food Agric. **10**, 135—144.
KING, H. G. C., and G. W. HEATH. Studies in leaf litter breakdown. III. The chemical analysis of small samples of leaf material and the relationship between leaf composition and disappearance (in preparation).
OVERGAARD NIELSEN, C., 1962. Carbohydrases in soil and litter invertebrates. Oikos, **13**, 200—213.

Address of the author: Dr. G. W. HEATH and MARGARET K. ARNOLD, Entomological Department, Rothamsted Experimental Station, Harpenden, Herts.

New address of Dr. G. W. HEATH: The Natural Environment Research Council, State House, High Holborn London W. C. 1.

Private address: Jacks Dell, Delmer End Lane, Flamstead, St. Albans, Herts.